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Spatial Variation in Tooth Shape of Miocene Populations of Carcharocles Megalodon Across Ocean Basins

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SPATIAL VARIATION IN TOOTH SHAPE OF MIOCENE POPULATIONS OF *CARCHAROCLES MEGALODON* ACROSS OCEAN BASINS

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By

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Maxwell John Bertsos ENTITLED Spatial variation in tooth shape of Miocene populations of *Carcharocles megalodon* across ocean basins BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Bertsos, Maxwell John. M.S. Department of Earth and Environmental Sciences, Wright State University, 2016. SPATIAL VARIATION IN TOOTH SHAPE OF MIOCENE POPULATIONS OF *CARCHAROCLES MEGALODON* ACROSS OCEAN BASINS

The extinct Lamniform species, *Carcharocles megalodon,* were some of the most geographically widespread apex predators in the fossil record. However, whether this cosmopolitan distribution was related to population level differences is unknown. The objective of this study is to assess whether variation in tooth morphology coincided with geographic dispersal. The underlying hypothesis is that variation in an aspect of functional morphology, such as tooth shape, suggests some level of population structuring. Detecting this relationship could potentially provide a mechanism that links population to functional relationships inherent in tooth morphology that may reflect period differences in ocean basins. This would offer a plausible explanation invoking selection as a mechanism for facilitation in their widespread occurrences, while not detecting a difference could have large scale population or selection implications. In this study, we used specimens housed in museum collections to assess morphological variation in upper anterior teeth (lingual view) from several locations spanning the modern day continents of North and South America. We used geometric morphometric techniques to describe tooth morphology and specifically tested for geographic differences in tooth shape by extracting morphometric axes from relative warp analyses

and subjecting these axes to ANOVA and MANOVA tests using an oceanic basin of origin as the grouping variable. Teeth from the Pacific and Atlantic Ocean basins were found to covary by geographic region statistically and visually with overlap dependent on the axis. The presence of variation in morphology indicates that there are drivers that differentiate selection of the cosmopolitan species, *C. megalodon*. A possible explanation of a driver can be analogue to modern Lamniforms, where consistent return to nesting or nursery sights and subsequent philopatry among mating adults would allow for differences. Further, it would be expected that a broader range of spatial selection of samples would also display this outcome; however, more testing with a more spatially diverse data set would be required.

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I. INTRODUCTION

Ecomorphological variation is a theme commonly focused on in biological studies that pertain to evolution, life history, and ecology. These variations can appear in otherwise widely dispersed populations as a result of the different environmental factors including food availability, habitation and reproduction space, and niche availability (Wainwright & Reilly, 1994). By determining the presence of variation it's possible to detect and understand intraspecific differences of a population from characteristics such as sex, maturity, size, and location. Variation, which can come in the form of innovations or reactions to environmental factors, can inform on how species or individuals within a population can affect or be affected by their associated ecology (Wainwright, 1991, Wainwright & Price, 2016). For instance, it is common for large apex predators, serving as a keystone species of a given ecosystem, to effect how the entire ecosystem functions at all levels (Pimiento & Clements, 2014; Pimiento, 2016). The more widespread a population of a given species the more diverse the ecological influences affecting the species on a whole.

C. megalodon (Agassiz, 1844) was the dominant marine predator during the Miocene and Early Pliocene. Size estimates have described *C. megalodon* as having reached 18 meters or more in length, making it the largest marine predator of its time (Gottfried et al., 1996; Pimiento & Balk, 2015). The species is the largest member of the

order Lamiformes, popularly known as the megatoothed sharks, which have since gone extinct.

There has been debate regarding the classification and lineages of *C. megalodon* and the megatoothed sharks, such as *C. auriculatus, C. angustidens* and *C. chubetensis* (Renz, 2002), and modern analogue *C. carcharias*, otherwise known as the Great White Shark. An older hypothesis claims that *C. megalodon* does not represent the megatooth shark lineage end member but is rather the direct relative of *C. carcharias* (Applegate & Espinosa-Arrubarrena, 1996; Gottfried et al., 1996; Purdy et al., 2001). Conversely, a newer hypothesis states that *C. megalodon* is the end species of the megatoothed lineage and that the great whites is a descendants of large extinct mako, *I. hastalis* (Cappetta, 1987; Casier, 1960, Ehret et al., 2012; Nyberg et al., 2006). Both hypotheses utilize morphometric similarities in shape and serration to lend support. With the continued suggested hypothesis regarding *Carcharocles megalodon*'s lineage still coming forward concerning the association with other megatoothed sharks (Shimada et al., 2016) the species will still maintain scientific significance.

Regardless, *C. megalodon* and the modern *C. carcharias* would appear to fill the same ecological niche, with a similar proposed morphology and dominant predatory habits (Pimiento et al., 2010). Other parallels between *C. megalodon* and other modern elasmobranches, such as mating and pupping habits, could be drawn upon for comparative purposes in intraspecific selections. Traditionally described as an apex predator, *C. megalodon* commonly made prey of marine mammals based on bite marks

on associated fauna and fossils (Gottfried et al., 1996; Aguilera & de Aguilera, 2004). *C. megalodon* served as an important facet of the food web during the period analogous to other larger marine predators today (Estes et al., 2011). While the species frequently hunted in the open ocean at various latitudes, they have also been found to have frequented warm shallow seas for hunting prey as well as giving birth and pupping in nursery sites (Pimiento et al., 2010).

C. megalodon, has been described as having a geographic range that achieved cosmopolitan status during the middle to late Miocene and into Pliocene before going extinct *c.* 2.6 Ma (Cappetta, 2012; Pimiento & Clements, 2014). Fossil occurrences for *C. megalodon* have been predominantly found in the Americas and Europe with occurrences throughout Asia and Australia being less abundant, but present (Ehret & Ebersole, 2014; Keyes, 1972; Pimiento, 2016, Yabe & Sugiyama, 1935). The fossils found in areas that would have been considered continental shelf at the height of *C. megalodon*'s distribution: the middle to late Miocene. Their dispersal has been documented alongside marine mammals they preyed upon, however, there is little known regarding any mechanisms that affects a cosmopolitan distribution (Pimiento, 2016). However, the distribution begs the question of how uniform the morphology was throughout the population considering natural or ecosystem barriers that may have exist. Considering the widespread extent of *C. megalodon*'s distribution, it is assumed that variation would be evident.

With the cosmopolitan geographic distribution that Pimiento and others (2016) described for *C. megalodon*, it is logical to question if there is any variation present as a result of the wide distribution. For many species it is common to determine how the ecology affects the morphology of various portions of the population. In terrestrial systems, natural barriers that exist drive morphological differences on the scale that can lead to speciation. Natural barriers in marine ecosystems, such as drastic changing in depth of water, do exist, but mechanisms for dispersal and large organisms' ability to transverse them diminish the effects on a population. Furthermore, marine populations become semi-isolated as a result of natural or biologic barrier of genetic drift (Palumbi, 1994). For the modern analogue of *C. megalodon* the genetic drift has been identified in species that are considered pelagic, widespread, or both. The closest modern analogue for *C. megalodon* is *C. carcharias* as both were dominant marine predators of large size expanses of open ocean or are otherwise pelagic. There have been studies showing that even though Great Whites exhibit these abilities, there are genetic differences in sub-populations in regions that are associated with those populations (Blower et al., 2012; Jogensen et al., 2009). Other sharks that exhibit wide geographic ranges but not the pelagic tendencies, such as the scalloped hammerhead, *Sphyrna lewini* (Duncan et al., 2006), spot-tail shark, *Carcharias sorrah,* (Giles et al., 2014), black-tip shark, *Carcharhinus limbatus* (Keeney et al., 2003), shortfin mako, *Isurus oxyrinchus* (Schrey & Heist, 2003) and the lemon shark, *Negaprion brevirostris* (Schultz et al., 2008) also display genetic variation across the population when compared to specific regions. The

genetic variation within a larger population would appear to be associated with modern shark species showing some degree of philopatry as a result of reproduction (Heuter et al., 2005).

Morphology is the result of the genetic makeup of a species, so morphological differences of a total population would affect the genetic makeup of a species. For modern cosmopolitan shark species the evidence of genetic variation has been identified and the link to morphological variation has been either similarly described or theorized (Blower et al., 2012; Schrey & Heist, 2003; Quatto et al., 2006). For the extinct *C. megalodon*, without the presence of genetic material, variation in the morphology of remains would be the next ideal source. By determining any morphological variation for *C. megalodon* it would be possible to claim the effects of biogeographic distribution on sub-populations of the species on a whole. Therefore, in order to detect the presence of any variation it is necessary to analyze fossil remains. Due to the predominantly cartilaginous skeleton of Lamniformes the dentition must be used for determining morphological variation. Furthermore, as a result of *C. megalodon* displaying highly heterodontic characteristics, the focus will be primarily on the teeth from the anterior section of the mouth.

The objective of this study was to examine the population of *C. megalodon* as it is present in the record of the North and South American continents and determine the presence of any morphologic variation, with a specific focus on each sample's oceanic

basin of origin as it relates to those two continents. The underlying hypothesis being that variation in an aspect of functional morphology, such as tooth shape, for *C. megalodon* suggests some level of population structuring.

II. METHODS

Teeth for this study were photographed by the authors or were submitted for inclusion from other collections. The majority of the teeth were photographed using a Nikon D3200 digital camera with a Macro Nikkor 60mm Macro Lens zooming lens with a 10 cm scale bar as a reference of sample size. Samples submitted by the other sources were collected using undefined digital camera hardware. Submitted teeth samples were placed with a scale bar that varied between a 10 cm bar to a 6 inch bar depending on the sample. The lingual view of each tooth was taken as a sample as it resulted in the most characteristic shape displayed for Lamniform species. Samples were collected from public collections including the South Carolina State Museum in Columbia, SC, Los Angeles Museum of Natural History in Los Angeles, CA, and Calvert Marine Museum in Solomons, MD as well as private collections including Dr. Gordon Hubbell of Gainesville, FL and Ms. Lisa Tohill of White Whale Quarry in Bakersfield, CA. Each of the collections included associated sets and individual teeth that ranged over large geographic areas encompassing the Atlantic and Pacific coasts of North and South America (Fig. 1). All information available regarding the locality, position, and age of each sample was recorded for comparative studies.

Geometric morphometric processes were used to describe the shape of each sample. This approach is a modern method of quantifying shape variation by using landmarks that are placed on an x-y plane with reference to a common scale. This method

is utilized in describing shape configuration relating to multiple linear measurements. Measurements were taken based on 11 predefined landmarks (Fig. 2), for both the labial and lingual views of each sample, that were chosen based on their reliability in the completion of the shape estimation. These landmarks represent the dominant characteristics present on a given sample regardless of the size or rotation so as to maintain that reliability. All images were digitized utilizing the tpsDig software (Rohlf, 2016) with determined landmarks applied to each.

General Procrustes Analysis (GPA) was utilized to superimpose the digitized individuals onto the mean reference shape. In doing such, any effects of scaling, rotation, or translation were removed. This allowed for individuals to be compared solely based upon differences in the shape (Zelditch et al., 2012) Relative warp analysis (RWA) was used to determine and access the gradients that contribute to shape variation among all individual samples. The relative warp scores were determined in consideration of thin plate splines (Querino et al., 2002; Jacquemin & Pyron, 2013) that were subsequently used in interpretation of shape configuration. Relative warp analysis is a principle component of the warp scores using eigenanalysis of the landmark positions; in doing such it is possible to discern the variation among individuals (Rohlf, 1993). Morphological analysis was performed using tpsRelw64 software (Rohlf, 2016). The RWA axes that displayed at least 5% of the variation, (the first 5 of the lower lingual warps and the first 6 of the upper lingual warps) were labeled as major RWA axes and subsequently were utilized for analysis.

Analysis of variance (ANOVA) was used to determine differences in the morphology that can be attributed to oceanic basin of origin. Each of the RWA axes that displayed a minimum 5% variation was considered. RWA axes displaying significance were compared considering oceanic basin of origin and visual representation of result recorded. Multivariate analysis of variance (MANOVA) with a Wilks' statistic was also performed to test for morphological differences associated with oceanic basin of origin or centroid size, the square root of the summed squared distacnces of each landmark to the centroid, of the sample. Primary RWA axes were treated as dependent response variables and the oceanic basin and centroid sizes of samples, as well as the interaction basin × centroid, were treated as independent variables. Separate MANOVAs were run for the upper and lower datasets.

General linear models (GLM) were used to identify significant effects from ocean basin and centroid size on each major RWA axis from both the upper and lower anterior data sets. Generalized linear models used the specific RWA axes as dependent response variables with ocean basin, centroid size, and the interaction between the two as independent variables. Those axes that provided significant results from ANOVA testing were included in the generalized linear models.

III. RESULTS

A total of 187 teeth were collected via photography or submitted for use as samples through the duration of this study. The total collection of samples includes 93 and 94 upper and lower anterior teeth, respectively.

The RWA axes that displayed a minimum of 5% of the total variance were taken into account. Analysis of variance produced three significant axes that accounted for nearly 42% of the upper anterior variance and three significant axes that accounted for nearly 55% of lower anterior variance. There were significant differences in shape via oceanic basin as well as centroid size for both upper and lower anterior teeth based on MANOVA of the RWA scores. A significant interaction of oceanic basin × centroid size was only present in MANOVA for lower anterior teeth (Table 1). For the upper anterior the centroid size was the stronger variable of morphology followed by the ocean basin. For the lower anterior ocean basin was the strongest with centroid size and the basin × centroid interaction following (Table 1).

A regressional visualization of the RWA axes that contributed as a result of meeting the minimum percent variation supports the results. The morphological differences between oceanic basins display more traditionally expected shape for elasmobranches from the Pacific while the Atlantic show a more deformed shape, especially relating to a pinching in the middle of the crown and a thinner root (Fig. 3). This variation in shape of teeth between the two basins is present in both the upper and lower anterior.

The regression visualization of the centroid size similarly showed differences between the minimum and maximum samples. For the upper anterior, larger teeth appeared to have the characteristic shark tooth shape while the smaller displayed a morphologically similar shape to the Atlantic regression visualization (Fig. 4). The lower anterior teeth minimum for centroid show a shape more commonly associated as being in a more lateral position in the mouth while the maximum display a normal shape except for a pinching of the right maximum root extent (Fig. 4).

Upper Anterior Teeth

The upper anterior ANOVA tests produced three significant axis considering ocean basin of origin; RW2, RW3, and RW6. The three axes also displayed significant axis in regard to the centroid size (Table 2). A comparative analysis of each axis that displayed the minimum variation was plotted with RWA extremes visualized (Figures 13, 14, 15) and it is shown that the Pacific and Atlantic teeth overlap but there is a difference in each cluster.

Differences in morphology by ocean basin and centroid size were determined from ANOVA for RW2 (24% variation). RW2 displays a more pointed tip of the crown to a more rounded tip, a thinning of the root, and the curvature of the cutting edges decreasing with increasing morphology (Fig. 5). Samples from both oceans display a positive slope in the GLM for RW2 and the centroid size (Fig. 7). Differences in morphology by ocean basin and centroid size were determined with ANOVA for RW3

(13% variation). RW3 resulted in increased morphologies in the size of the root as well as a slight increase in the crowns width (Fig. 5). GLM for RW3 resulted in a negative slope for the Pacific and a positive slope for the Atlantic when comparing RW3 to centroid size (Fig. 8). Morphological differences by ocean basin and centroid size were found in consideration of ANOVA for RW6 (5% variation). RW6 resulted in an increased gradient of morphologies with an increase in the roundness of the tip, a flatter root to crown contact, and a broader tooth (Fig. 5). The GLM for RW6 displayed a negative response per unit of centroid size in both the Atlantic and Pacific (Fig. 9)

Lower Anterior Teeth

The lower anterior ANOVA tests produced three significant axes considering ocean basin of origin; RW1, RW3, and RW4. RW1 and RW4 did not display similar significance regarding centroid size with ANOVA though the GLM for RW4 does display significance. RW3 also represents a significant axis for centroid size in ANOVA and GLM (Table 3). A comparative analysis of each axis that displayed the minimum variation was plotted with RWA extremes visualized (Figures 16, 17, 18) and it is shown that the Pacific and Atlantic teeth overlap but there is a difference in each cluster.

Differences in morphology by ocean basin were determined from ANOVA and GLM for RW1 (37% variation). RW1 resulted in thinning of the shape of the tooth overall, the root becoming marginally thicker as the lateral extremes are drawn in and a rounding of the tip of the crown (Fig. 6). The GLM for RW1 that compared it to centroid

size displayed a negatively sloping relationship for both oceans (Fig. 10). Differences in morphology by ocean basin and centroid size were detected using ANOVA and GLM for RW3 (10% variation). RW3 resulted in a thinning of the root laterally and vertically as well as rounding of the tip of the crown with increased morphologies (Fig. 6). The RW3 Atlantic samples display a clearly positive trend while the Pacific samples do slope positively but the trend is much less pronounced (Fig. 11). Differences in morphologies by oceanic basin were detected by ANOVA and GLM for RW4 (8% variation). RW4 resulted in a thinning of the root laterally along with a thickening of the crown across the line where the mid-point landmarks were placed with increased morphologies (Fig. 6). The GLM for RW3 Atlantic samples display an increase in morphology with increased centroid size while the Pacific samples display a negative trend over an increase in centroid size (Fig. 12).

IV. DISCUSSION

The results of this study indicate that the oceanic basin of origin contributed to morphological variation of the cosmopolitan specie, *C. megalodon*. Analysis indicates that, for upper and lower anterior teeth, ocean basin of origin contributed more to the morphological variation compared to centroid size. However, the degree of contribution between oceanic basin and centroid size was close for some of the axes which suggest that while basin of origin is a primary driver of variation between the Atlantic and Pacific grouping of *C. megalodon* population the morphology of an individual tooth is not clear cut. The conclusions would appear to agree with studies relating to modern sharks showing genetic variations within a total population (Blower et al.,2012; Duncan et al., 2006; Pardini et al., 2001). The one caveat to these findings is incomplete nature of the data set on a whole missing other cosmopolitan regions and the differences in the scale of variation could change dramatically if considered.

The presence of morphological variation in centroid size is not unusual as the presence of teeth from adults in various stages of development could contribute to shape differences. Juvenile teeth were largely left out of this study as a result of ontogenic variations occurring through the developmental cycles. While the focus of this study was not on the variation as a result of size, the general linear models comparing the RWA axes to size did support that there are significance differences between the two basins of focus. Other usual factors that could contribute to variation, such as sex, were not

considered because of the large sample size as well as lack of information for the specimens collected.

The cause of the diversity in morphological variation in *C. megalodon* between the Atlantic and Pacific populations can only be hypothesized at this point. During the time of maximum geographic distribution for *C. megalodon* in the middle to late Miocene the position of the continents were proximal to modern locations. With the Isthmus of Panama yet to close there would have been an open seaway between the two oceanic basins (Bartoli el al., 2005; Coates & Obando, 1996). This opening would have allowed for an easy interchange between the two populations. However, this study has detected variation between sample populations from each basin so there must have been some drive causing the morphological differences.

A simple explanation for this variation may involve *C. megalodon* returning to nursery sites to spawn new offspring. These sites would be useful as they would allow the sharks to pup and have their young able to grow to adulthood in relative safety (Heupe et al., 2007). There has been work showing evidence for the existence of *C. megalodon* nursery sites, mainly through the discovery of large amounts of juvenile teeth (Pimiento, 2010; Pimiento et al., 2013). Evidence for modern elasmobranch nursery locations has been studied and definitions have been put forth (Blower et al., 2012; Domier, 2012; Domier & Nasby, 2013; Pardini et al., 2001). A reoccurring characteristic that was described in modern elasmobranch nurseries was the use of a given nursery site year after year, and the return to said location of reproductive adults, as well as evidence of adults

remaining in the area for an extended time (Duncan et al., 2006; Giles et al., 2014; Keeney et al., 2003). With evidence regarding the presence of *C. megalodon* nursery sites, analogous information from the sites of modern sharks suggests that *C. megalodon's* morphology is influenced by its nursery site of origin. Subsequently, if a sub-population of the species regularly returned to the same nursery areas within a give oceanic basin, then morphological variation between basin populations is plausible. Returning to nursery sites has been suggested as one of the primary drivers behind species separation in modern marine species (Heist, 2004; Heuter et al., 2005; Palumbi, 1994) including sharks (Schrey & Heist, 2003). Therefore the variation present within this study regarding *C. megalodon* could be similarly hypothesized.

Ultimately, in order to truly grasp the degree to which morphological variation in *C. megalodon* can be associated with its cosmopolitan distribution, a true cosmopolitan data set would first be required. A data set that included a larger pool of samples including those from associated sets as well as a diversity of localities for a given region, ideally at the height of the geographical distribution: the middle Miocene (Pimiento, 2016). With wider sampling, any morphological variance of full cosmopolitan distribution will provide a better idea of what drives those differences. However, regarding this study, and the two oceanic basins connected to the American continents serving as parameters, morphological variation is present in the distribution of *C. megalodon*. As a result of a wide spatial distribution of samples, this ocean basin variation can be reasonably assumed to reflect a cosmopolitan variation.

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Figure 1: Geographic locations of *C. megalodon* localities included in this study. Closed circles represent sites along the Pacific Ocean basin and open squares represents sites associated with the Atlantic Ocean basin. California; Tremblor Fm., Shark Tooth Hill, White Whale Quarry, middle Miocene. Peru; Pisco Fm., Cerro Colorado, Late Miocene. Chile; Bahia Inglesa Fm., Northern Atacama Desert, late Miocene. Florida; Bone Valley Fm., Bone Valley Region, Venice Beach, middle to late Miocene. South Carolina; Lower Yorktown Fm., Beaufort Co., Broad River, late Miocene. North Carolina; Lower Yorktown Fm., Lee Creek Mine, Aurora, middle to late Miocene. Maryland; Calvert Fm., Calvert Cliffs, Miocene.

Figure 2: Location of 11 morphology landmarks on *C. megalodon* upper (Left) and lower (Right) anterior teeth. Landmarks consistently placed clockwise starting at tip if the crown (1), halfway between points 1 and 11 (2), halfway between points 1 and 6 (3), junction point between crown and root (4), outer most tip of root lobe (5), center of the outer edge of the root (6), outer most tip of root lobe (7), junction point between crown and root (8), halfway between points 1 and 6 (9), halfway between point 1 and 11 (10), center of the inner edge of the root (11). Both samples courteous of Dr. Gordon Hubbell; (Right) upper anterior, AF/NC-97-37T (UF311000) and (Left) lower anterior, AF/NC-97-37T (UF311000).

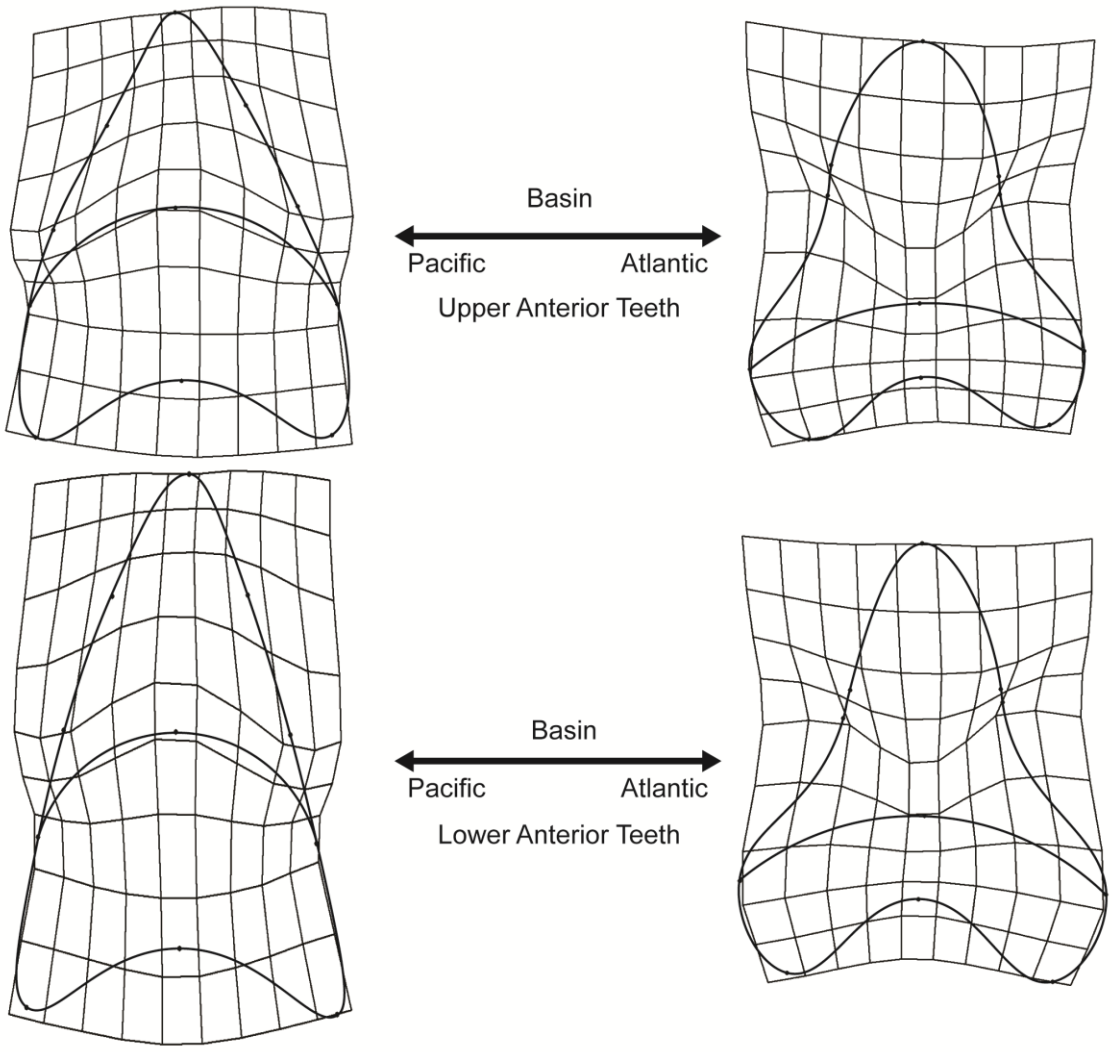

Figure 3: A visualization of the regression of the upper (top) and lower (bottom) anterior teeth with the extremes corresponding to the oceanic basin of origin. The visualization is represented with a 10× range to maximize morphological differences.

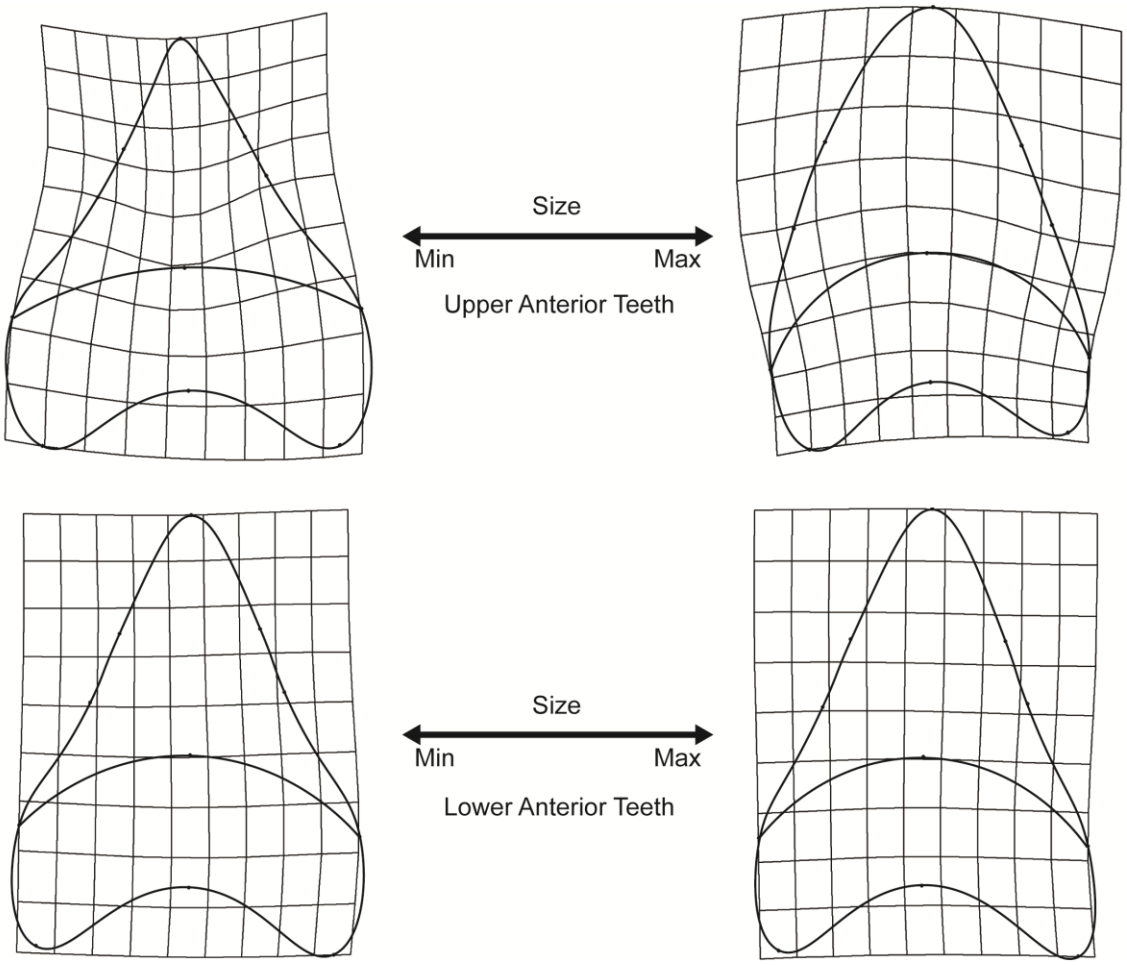

Figure 4: A visualization of the regression of upper (top) and lower (bottom) anterior teeth with extremes corresponding to differences in centroid size. The visualization is represented with a 3× range to maximize morphological differences.

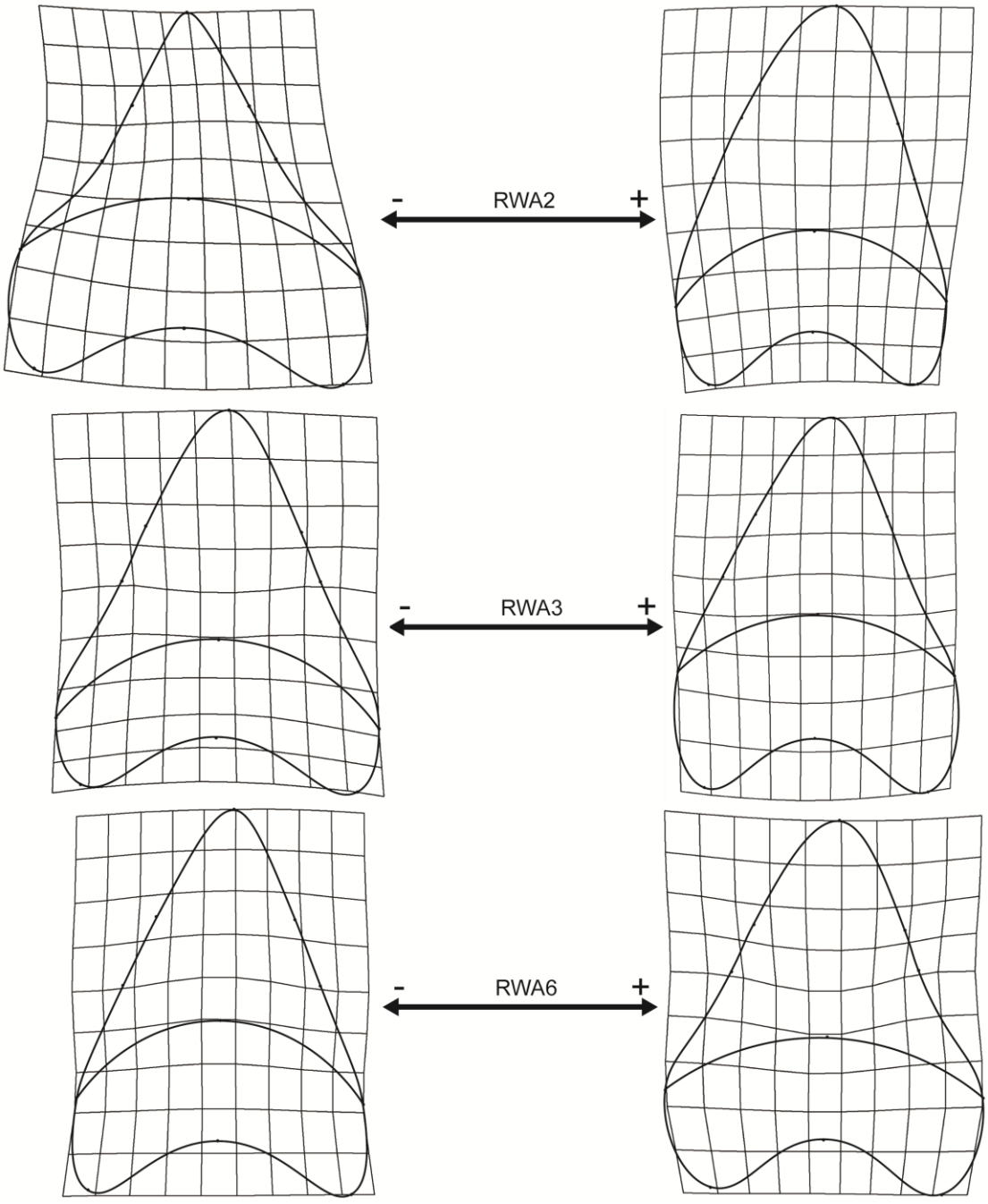

Figure 5: Thin plate spline deformation grids relative for consensus image for three morphological axes that displayed minimum percent variation for the upper anterior teeth. See text for details.

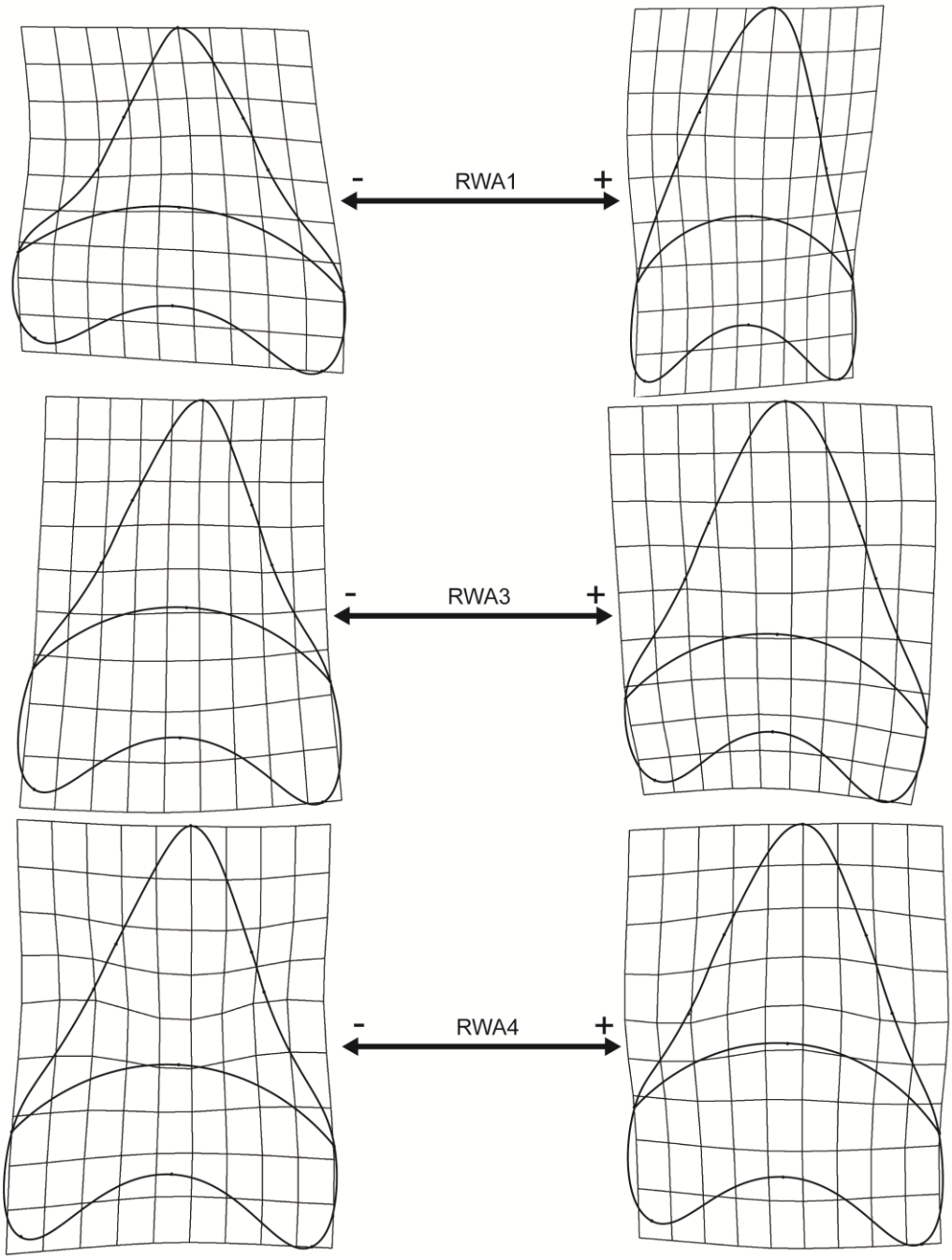

Figure 6: Thin plate spline deformation grids relative for consensus image for three morphological axes that displayed minimum percent variation for the lower anterior teeth. See text for details.

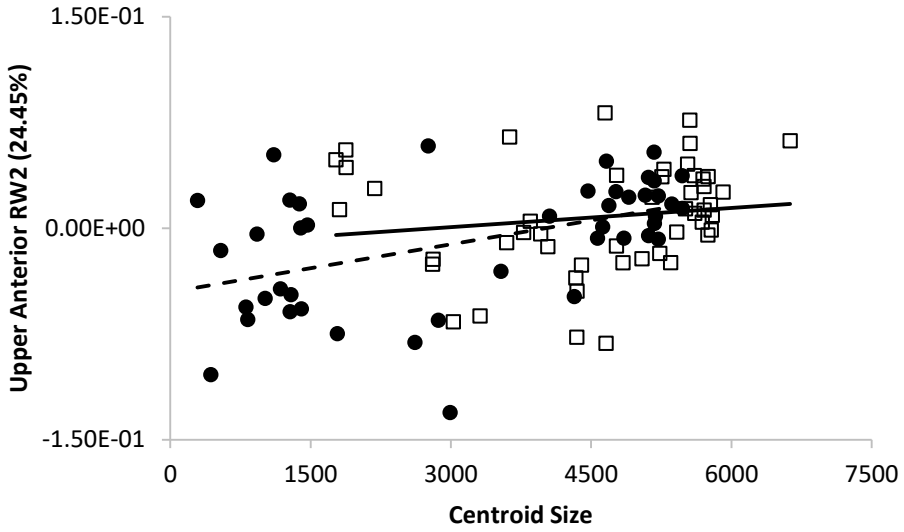

Figure 7: Scatterplot of upper anterior RW2 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

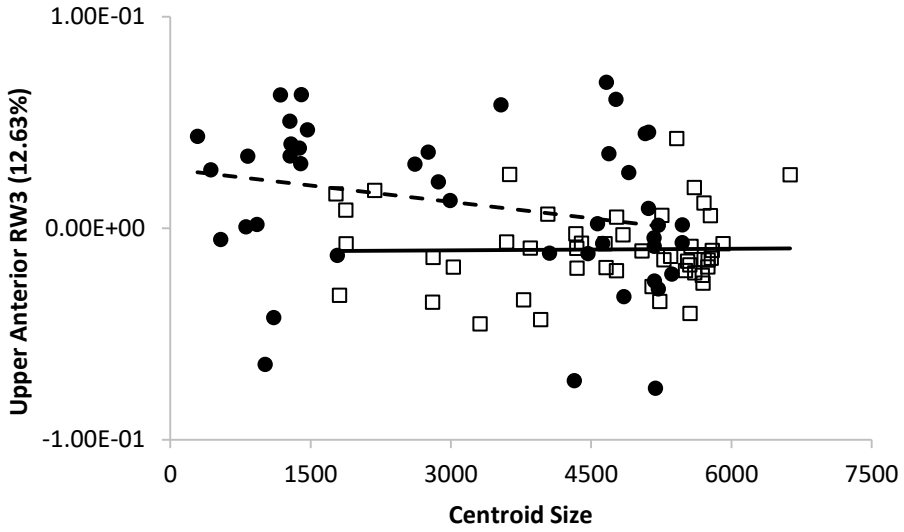

Figure 8: Scatterplot of upper anterior RW3 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

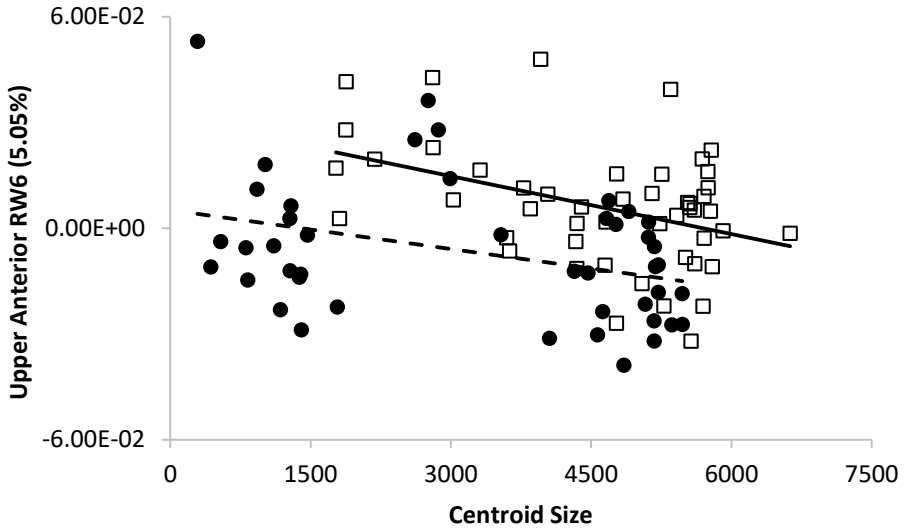

Figure 9: Scatterplot of upper anterior RW6 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

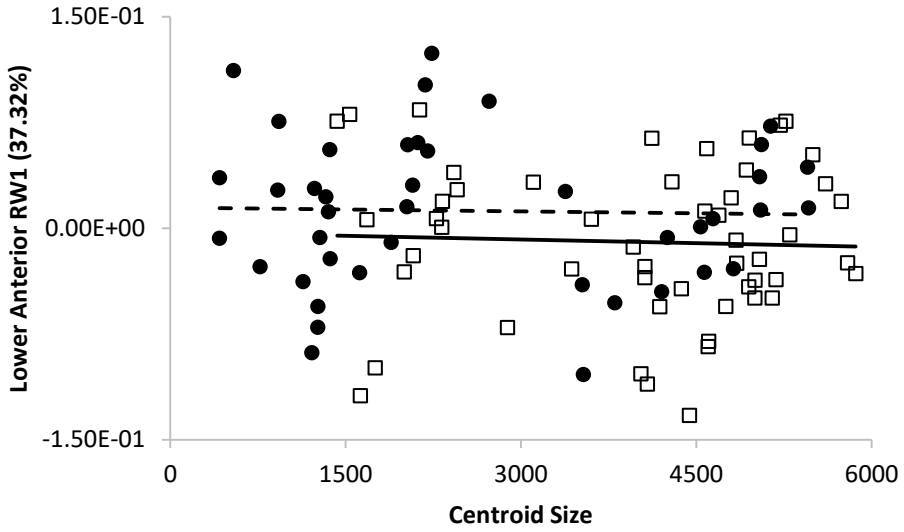

Figure 10: Scatterplot of lower anterior RW1 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

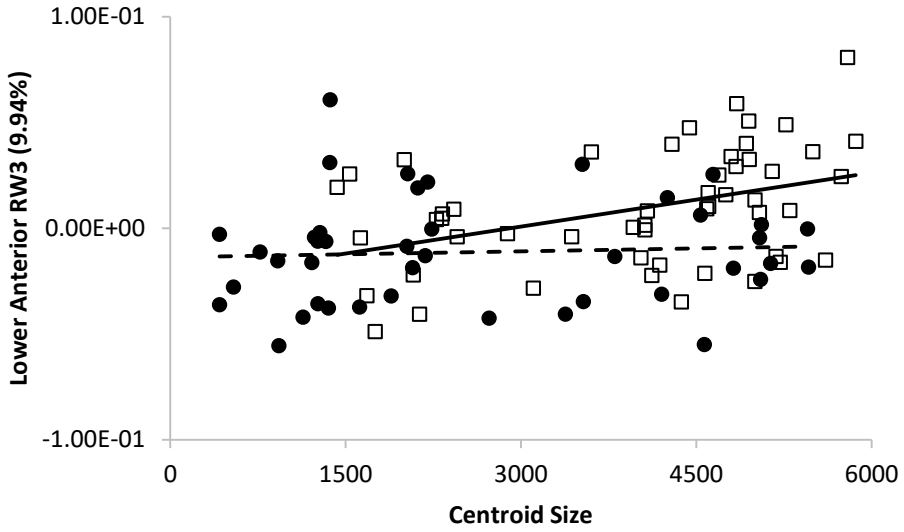

Figure 11: Scatterplot of lower anterior RW3 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

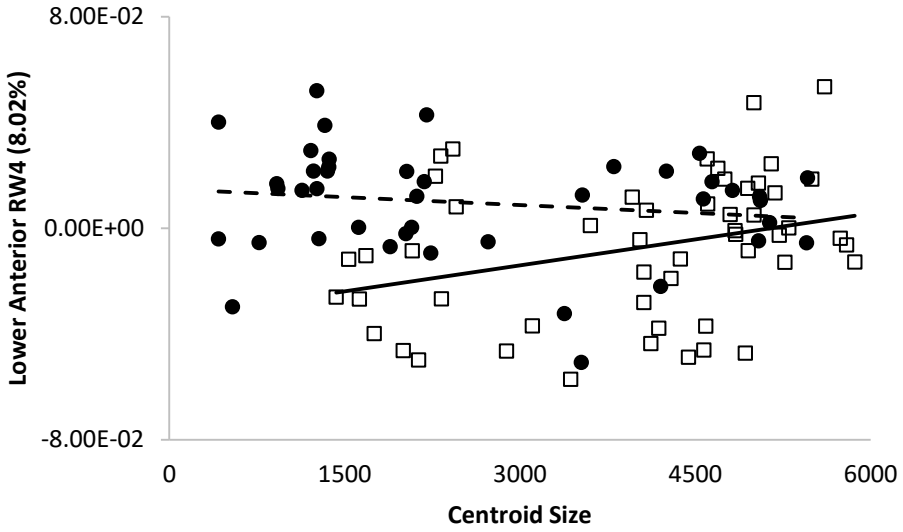

Figure 12: Scatterplot of lower anterior RW4 and centroid size with regressions for oceanic basin of origin. Closed circle indicate Pacific samples, open squares indicate Atlantic samples, solid line indicates the mean shape of Atlantic samples and dotted line indicates the mean shape of pacific samples.

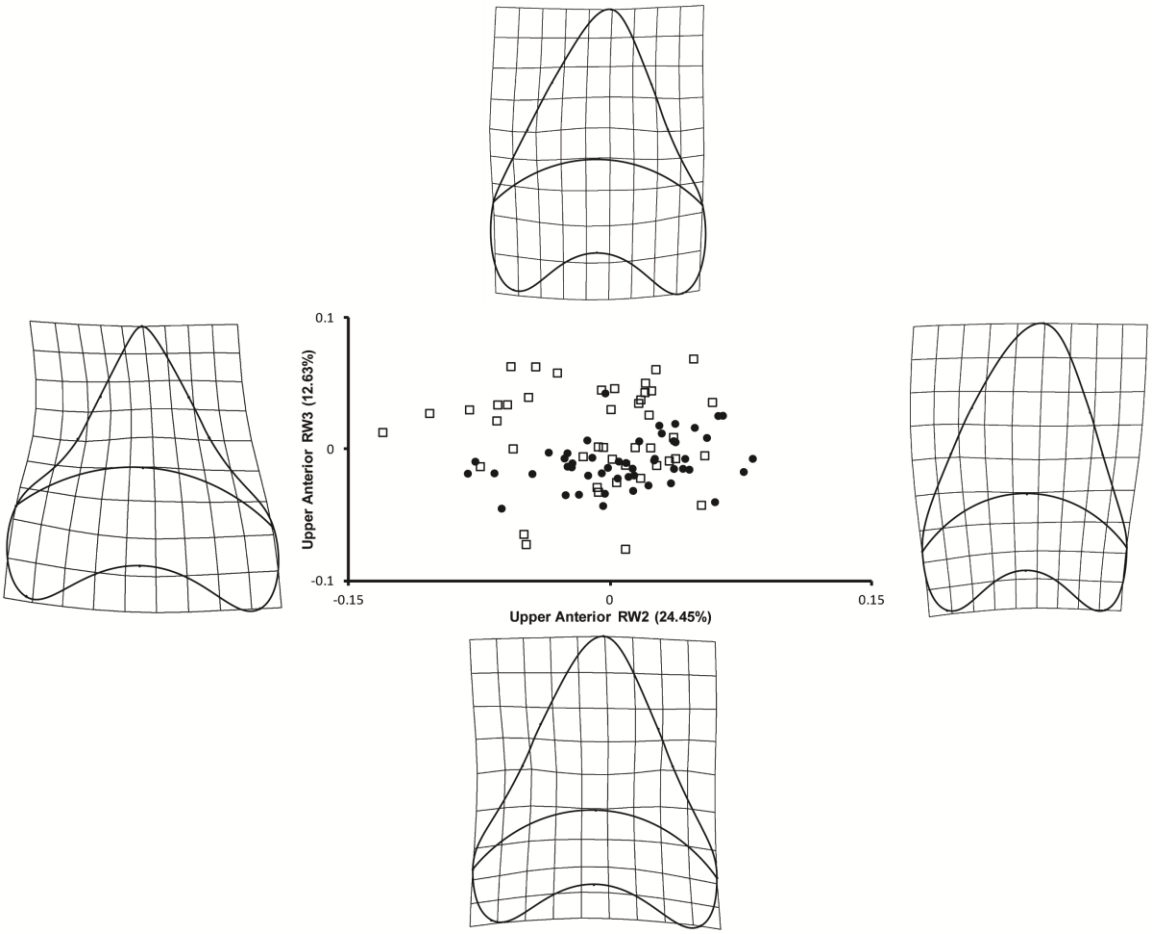

Figure 13: Comparative scatter plot of upper anterior RW2 and RW3. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

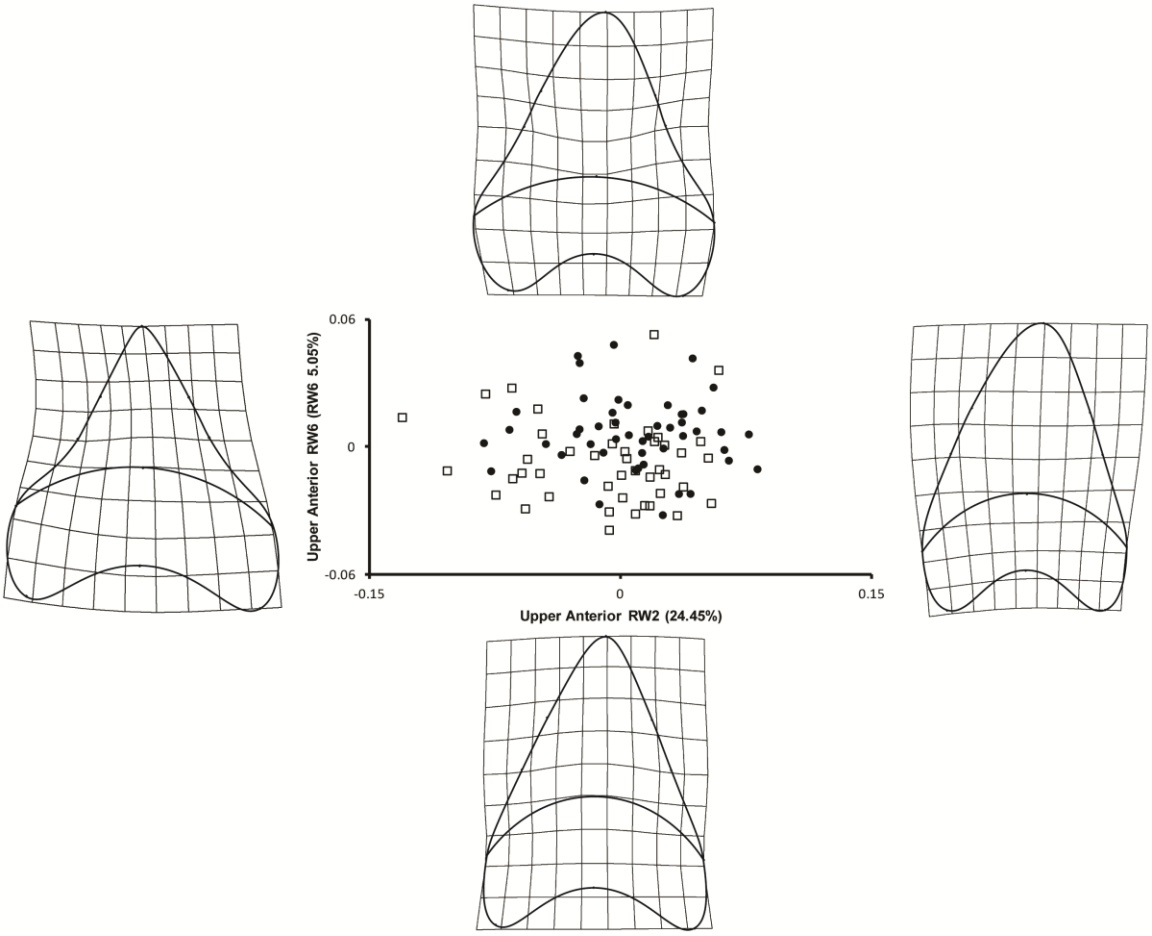

Figure 14: Comparative scatter plot of upper anterior RW2 and RW6. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

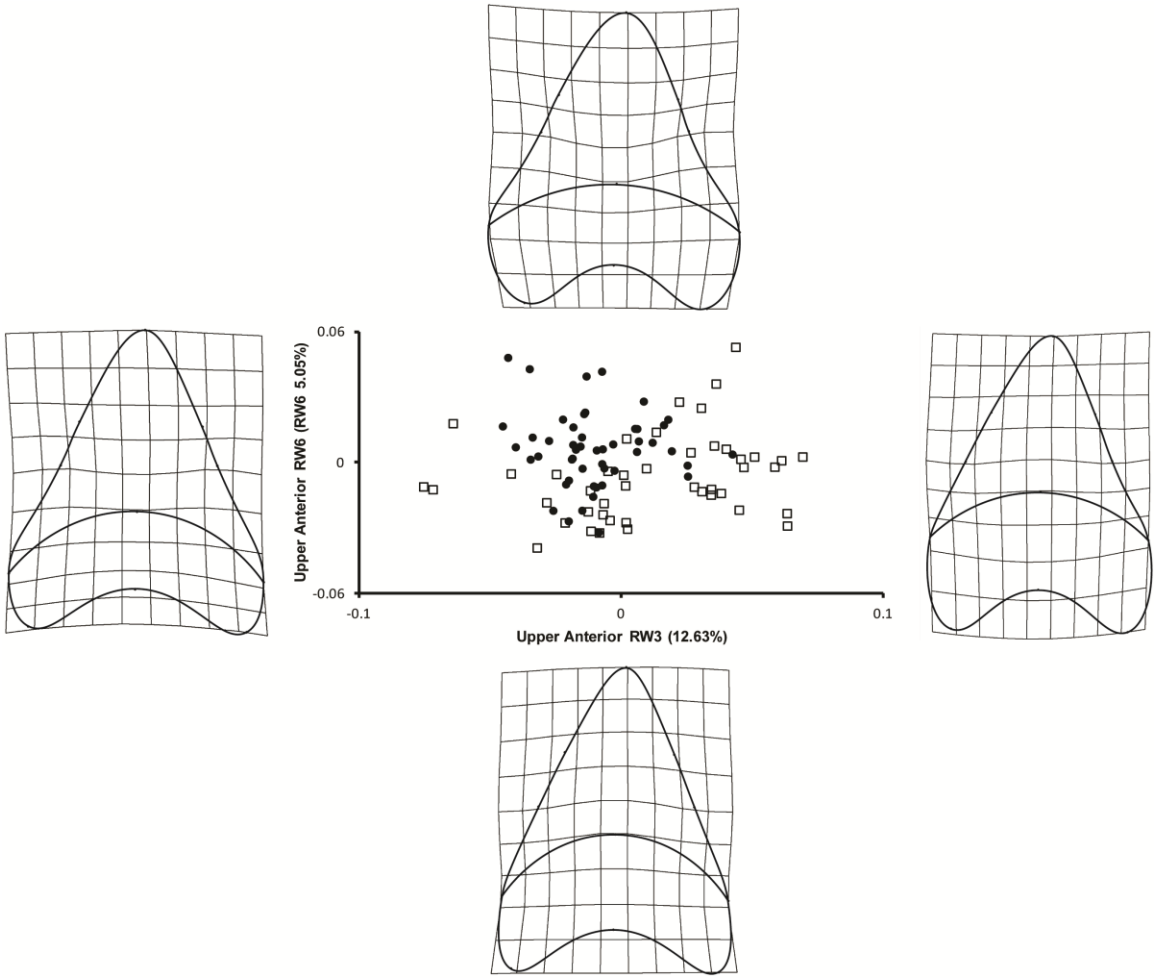

Figure 15: Comparative scatter plot of upper anterior RW3 and RW6. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

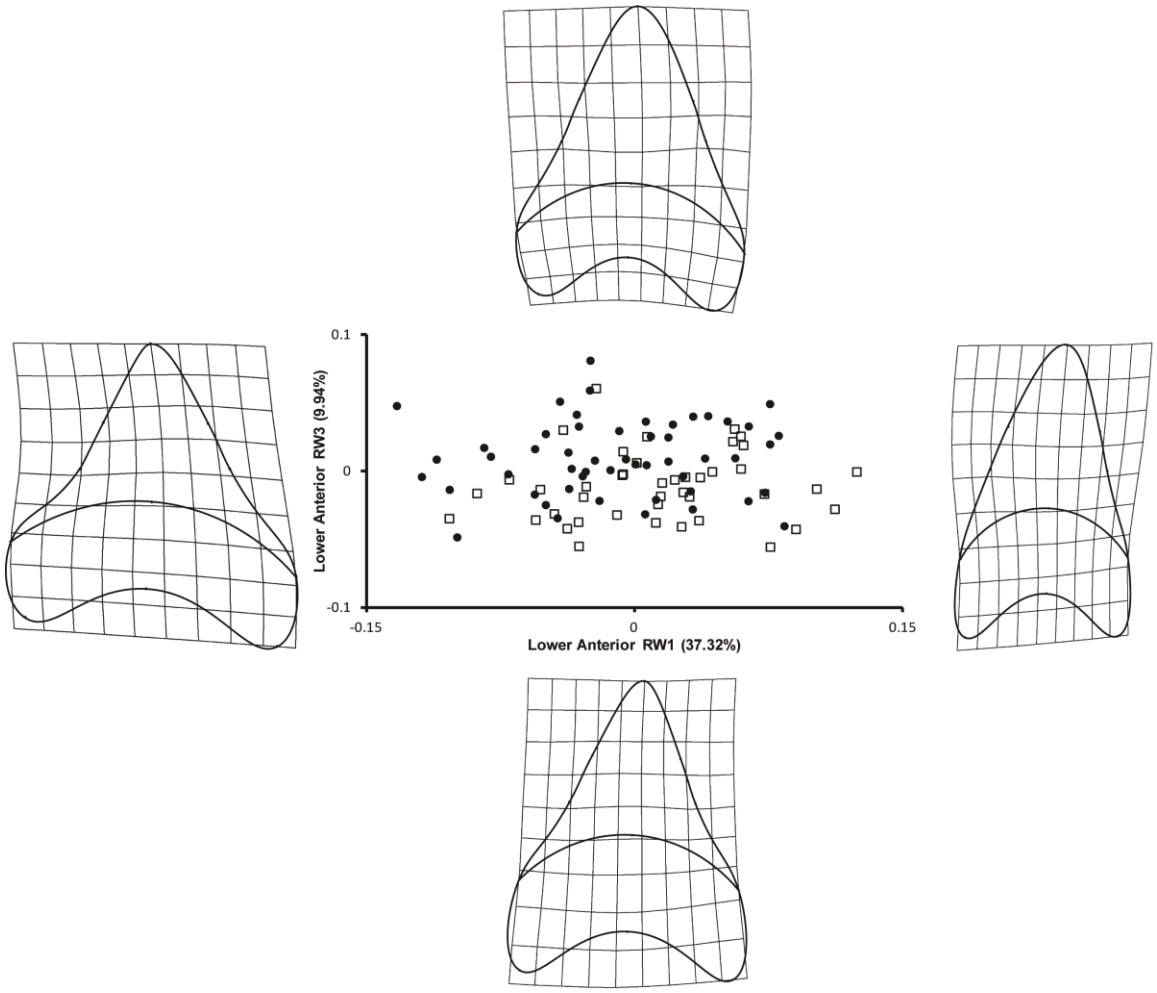

Figure 16: Comparative scatter plot of lower anterior RW1 and RW3. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

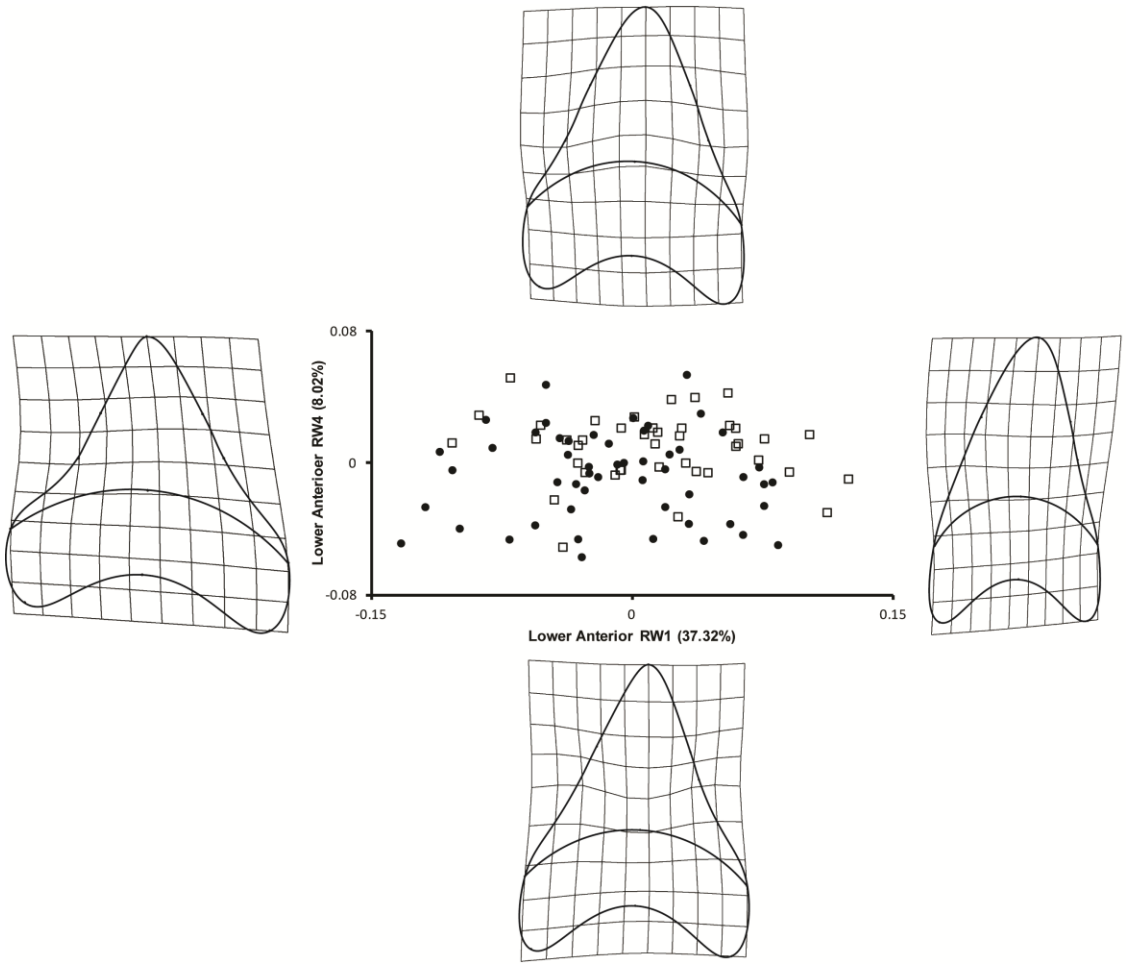

Figure 17: Comparative scatter plot of lower anterior RW1 and RW4. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

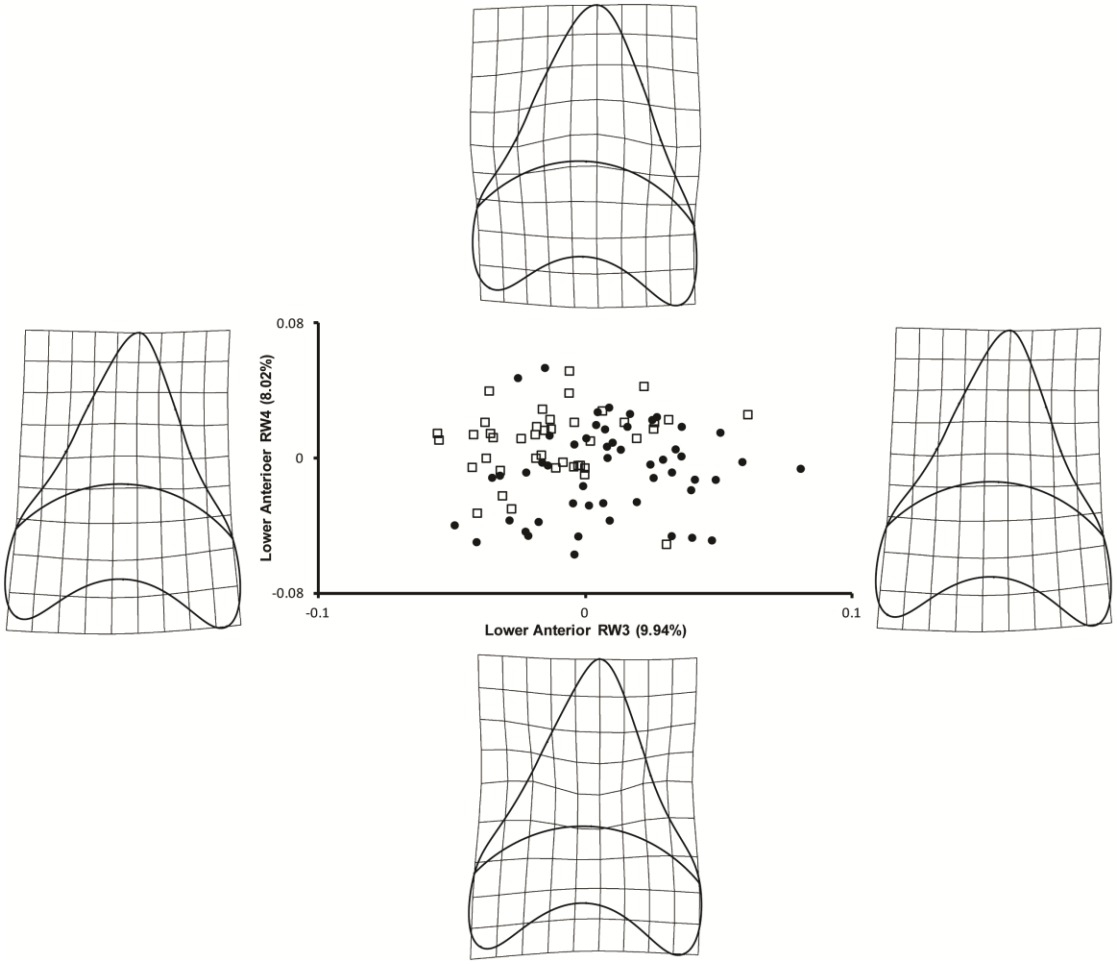

Figure 18: Comparative scatter plot of lower anterior RW3 and RW4. Extremes of each axes are marked with visual representation from tpsRelw. Closed circles represent Pacific teeth and open squares represent Atlantic teeth.

Table 1: MANOVA results of upper and lower anterior data sets. Basin of origin and centroid size were strong predictors of morphology for the upper and lower anterior teeth. The interaction of basin × centroid as served as a predictor.

	Effects	Wilks λ	*F*	df	*P*
Upper Anterior	Basin	0.7068	5.8088	6,84	<0.001
	Centroid	0.6098	8.9588	6,84	<0.001
	Basin × Centroid	0.891	1.7127	6,84	0.128
Lower Anterior	Basin	0.6968	7.4845	5,86	<0.001
	Centroid	0.7901	4.5691	5,86	<0.001
	Basin × Centroid	0.788	4.627	5,86	<0.001

Table 2: ANOVA Table of GLM results of upper anterior individual morphology axes with ocean basin, centroid size, and the interaction basin × centroid as independent variables.

Source	SS	df	MS	*F*	*P*
RWA1					
Basin	0.00121	1	0.0012	0.5661	0.4538
Centroid	0.00187	1	0.00187	0.8784	0.3512
Basin × Centroid	0.00025	1	0.00025	0.119	0.7309
Residual	0.18942	89	0.00213		
RWA2					
Basin	0.0067	1	0.0067	4.374	0.03934
Centroid	0.01831	1	0.018312	1.9512	0.00084
Basin × Centroid	0.00235	1	0.00235	1.5335	0.21885
Residual	0.13637	89	0.00153		
RWA3					
Basin	0.0106	1	0.010596	3.4897	0.00041
Centroid	0.00249	1	0.00249	3.1755	0.07816
Basin × Centroid	0.0015	1	0.0015	1.9128	0.17011
Residual	0.06991	89	0.00079		
RWA4					
Basin	0	1	2.00E-07	0.0003	0.98659
Centroid	0.00705	1	0.007052	1.8192	0.00089
Basin × Centroid	0.00184	1	0.00184	3.09	0.08221
Residual	0.0531	89	0.0006		
RWA5					
Basin	2.00E-06	1	2.00E-06	0.0042	0.9486
Centroid	8.00E-06	1	7.70E-06	0.0159	0.9001
Basin × Centroid	0.00128	1	0.00128	2.65	0.1071
Residual	0.04296	89	0.00048		
RWA6					
Basin	0.00375	1	0.00375	13.0128	0.00051
Centroid	0.0042	1	0.0042	14.5626	0.00025
Basin × Centroid	0.00017	1	0.00017	0.5763	0.44978
Residual	0.02566	89	0.00029		

Table 3: ANOVA Table of GLM results of lower anterior individual morphology axes with ocean basin, centroid size, and the interaction basin × centroid as independent variables.

Source	SS	df	MS	*F*	*P*
RWA1					
Basin	0.01123	1	0.01123	3.7296	0.0566
Centroid	0.00033	1	0.00033	0.1082	0.743
Basin × Centroid	3.10E-05	1	3.10E-05	0.0104	0.919
Residual	0.27091	90	0.00301		
RWA2					
Basin	0.00135	1	0.00135	0.9022	0.34474
Centroid	0.00151	1	0.00151	1.0118	0.31717
Basin × Centroid	0.00718	1	0.00718	4.7988	0.03106
Residual	0.1346	90	0.0015		
RWA3					
Basin	0.00972	1	0.00972	14.8194	0.00022
Centroid	0.00365	1	0.00365	5.5722	0.02048
Basin × Centroid	0.00279	1	0.00279	4.2624	0.04184
Residual	0.059	90	0.00066		
RWA4					
Basin	0.00682	1	0.00681	12.3578	0.00069
Centroid	0.00066	1	0.00066	1.1908	0.27809
Basin × Centroid	0.00357	1	0.00357	6.473	0.01266
Residual	0.04963	90	0.00055		
RWA5					
Basin	0.00021	1	0.00021	0.43	0.51365
Centroid	0.00704	1	0.00704	14.4987	0.00026
Basin × Centroid	0.00361	1	0.00361	7.4445	0.00765
Residual	0.0437	90	0.00049		